

Trends in milk production, calving rate and survival of cows in 14 Irish dairy herds as a result of the introgression of Holstein-Friesian genes

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Abstract

Trends in milk production, calving rates, and survival were monitored on a potential 5580 primiparous and multiparous Holstein-Friesian dairy cows across 14 Irish seasonal spring-calving dairy farms between the years 1990 and 2001. Over this period calving rate to first service (CALV1) reduced by 0.96% per year (55 to 44%; $P < 0.001$), calving rate to first and second service (CALV12) reduced by 0.84% per year (77 to 70%; $P < 0.001$) and herd average parity number reduced by 0.10 lactation per year (4.3 to 3.5; $P < 0.001$). The proportion of North American Holstein Friesian (NAHF) genes in the cows increased by 5.5% per year (8 to 63%; $P < 0.001$), while pedigree index for milk yield (PI_{MILK}) of the cows increased by 25 kg per year ($P < 0.001$). The predicted difference of the sires of the cows for calving interval and survival increased by 0.5 days ($P < 0.001$) and reduced by 0.12% ($P < 0.001$) per year, respectively. A negative association was found between increased phenotypic milk yield, NAHF and PI_{MILK} and reduced calving rates as assessed by CALV1 and CALV12. Increased proportion of NAHF genes exhibited a negative effect on survival ($P < 0.001$) whereas increased levels of heterosis had a positive impact on survival ($P < 0.001$). The results of the present study indicate that in seasonal calving herds in Ireland a need for direct selection on traits related to fertility and survival is required to arrest and reverse the declining trends in calving rates and survival.

Keywords: calving, fertility, genetic change, Holstein-Friesian, survival.

Introduction

Milk production systems in Ireland are predominantly pasture-based and involve seasonal calving (Dillon *et al.*, 1995). In a typical seasonal herd in Ireland, breeding starts on a fixed calendar date between late April and early May. The key reproductive objective is to achieve a high pregnancy rate in the shortest period of time after the start of the breeding season in order to achieve a concentrated calving pattern the following season (O'Farrell, 1994). Achieving this objective is required to maintain a calving interval of around 365 days. Surveys carried out in the 1960s and 1970s (Crowley *et al.*, 1967; Cunningham *et al.*, 1978; Roche *et al.*, 1978) illustrated that calving rates to first service were high ($>60\%$) and that culling rates for infertility were low ($<10\%$). Calving intervals of less than 365 days were readily obtained. A review of herds participating in the Dairy Management Information System (DairyMIS; Crosse, 1991) by O'Farrell and Crilly (2001) showed that calving rate to first service had fallen to 53% in 1991 and further eroded to 49% by 1996. More recently Evans *et al.* (2002)

reported a pregnancy rate to first service of 48% across 74 spring calving herds in the 1999 calving season.

Up to the mid 1980s the predominant breed of dairy cow in Ireland was the British Friesian. This had been graded up from the Dairy Shorthorn beginning in the late 1960s. Over the last 20 years in both the UK and Ireland the use of North American Holstein Friesian (NAHF) genetics has dominated, increasing in sires used from 10% in 1977 to 80% in 1998 (Simm, 1998). The initial imports of NAHF genetics were from Canada and the USA but later importations included European germplasm. However, it is documented that the European Holstein traces back to a similar North American origin. The popularity of the NAHF was most likely due to its substantially increased productivity over native breeds. Aggressive selection for increased milk yield in the NAHF has resulted in a now, well documented negative effect on cow fertility (Hoekstra *et al.*, 1994; Pryce and Veerkamp, 2001; Evans *et al.*, 2002; Pryce *et al.*, 2004). Genetic parameters predict an antagonistic genetic relationship between milk yield and reproductive traits (Pryce *et al.*,

1998; Evans *et al.*, 2002). Pryce *et al.* (1998) estimated an increase in the calving interval by 5 to 10 days per 1000-kg milk yield when selection was based on milk production traits only. These values are supported by the results from controlled experiments comparing genetic groups across feeding systems (Buckley *et al.*, 2000; Kennedy *et al.*, 2003). It has been suggested that the increased milk yield associated with upgrading/substitution of the Friesian with the NAHF may explain a proportion of the decline in reproductive performance (Royal *et al.*, 2002).

The objective of this study was to quantify the phenotypic and genetic trends in milk production, calving rate and survival in 14 Irish seasonal spring calving dairy herds, which were participating in DairyMIS over the period 1990 to 2001. The extent to which the decline in calving rate was associated with the introgression of NAHF genes, increased genetic merit for milk yield and increased phenotypic yield was elucidated.

Material and methods

DairyMIS is a recorder-based computerized system collecting detailed information regarding stock, farm inputs, production and insemination and calving events on a monthly basis (Crosse, 1991). Between 26 to 28 herds participated in DairyMIS in any one year, 18 participated in all years from 1990 to 2001. Of the 18 herds, four had a split autumn/spring calving pattern which were subsequently omitted from the analysis when the criteria was set at a minimum of 95% of cows in the herd calving between January and June in any calendar year. Spring-calving herds were the category of interest in this study as it is by far the predominant calving system in Ireland. The mean herd size of the remaining 14 herds was 103 cows with a range from 42 to 322 cows. Data included information both at an individual cow level and at a herd level. Data handling was carried out using Microsoft Access 97. A unique herd and cow identifier was attached to each record. Data handling included the identification of anomalies such as duplicate records, incomplete records, as well as creating the specific production and calving performance related traits to be analysed.

Calving and insemination parameters

Five calving/fertility performance traits were obtained as a function of calving and insemination observations and used in the creation of a CALVING data set. The traits generated included calving rate to first service (CALV1), calving rate to first and second service (CALV12), number of services per cow (NS), calving to first service interval (CSI) and inter calving interval (ICI). Subsequent calving dates were used to assign a positive or negative pregnancy result to a recorded service event. When a subsequent calving at an interval of no more than 300 days followed a service, the animal was deemed to have conceived to that service. Where two services were recorded within an interval of 4 days or less, they were considered the same event and the date of service attributed to the first event. Where a service was followed by a further service at an interval of 5 days or

greater, the initial service was considered to have failed. If a calving event occurred more than 300 days after the last recorded service event, the cow was assumed to have conceived to an unrecorded service (most likely a natural mating) and the last recorded service was deemed to have failed. Unrecorded services were most likely to have occurred in the latter stages in the breeding season as the common practice in these herds was to initially carry out artificial insemination for a period of 8 to 10 weeks from the start of breeding and subsequently use natural mating for the remainder of the breeding season. Approximately 6% of cows calved more than 300 days after the last recorded service. Cows with a documented abortion in a particular year were not included in the analysis (1% of cows in the herds). The DairyMIS system records all sale dates and reasons for sale. The record of a cow sold for reasons other than infertility or who died, less than 300 days after the last recorded service was not included in the analysis as there was no way of determining her pregnancy status at time of removal from the herd (3.7% of all cows which received at least one insemination in the year in question). When cows were sold less than 300 days after the last recorded service due to documented infertility then all services recorded prior to sale were deemed unsuccessful and included in the analysis.

Calving dates were categorized into three calving periods: January and February, March, and April or later. Calving dates between June and December were excluded (1.8% of records). This edit was undertaken to restrict the data set to spring calving cows only, which is the dominant season of calving in Ireland and the category of interest in the present study. The resulting data set CALVING contained 14 019 insemination records on 4434 individual cows for CALV1 and 13 311 records on 4370 individual cows for CALV12. The reduction in number of records between CALV1 and CALV12 was due to a decision rule implemented for both CALV1 and CALV12 whereby an animal was censored if that animal was sold less than 300 days after her last recorded service with a documented sale reason other than infertility. This was implemented as there was no way of determining if that animal was pregnant at the time of removal from the herd.

Milk production

Individual test day milk records, parity and drying off dates were obtained from the Irish Dairy Recording Co-operative for all cows in the participating herds. The herds were milk recorded on a monthly basis. Parity number was verified with the DairyMIS calving files. Parity was categorized as one, two or three and greater. Lactation length for each cow was calculated as the differential between calving date and recorded dry-off date. Individual lactation milk yield (MILK_{YLD}) was estimated as the mean of at least six test day records multiplied by the lactation length. The original file contained 10 189 lactation records with a subsequent dry-off date. After imposing a minimum requirement of six test dates and a valid dry-off date, the data set MILK contained 9383 records on 3179 individual cows. The method used was thought to be sufficiently accurate given the number of lactations available, the routine monthly testing, and relatively short lactation lengths.

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Possible reasons for unavailability of some milk yields may have been due to a combination of farmer decision to milk record only a certain proportion of the herd in the initial years of the study period, but also to a lack of recording of dry-off dates by milk recording organizations. Whole herd milk production levels were also available for all herds in all years from DairyMIS. These yields were calculated on a monthly basis as the sum of the milk supplied to the manufacturing factory, plus milk fed to calves and milk withheld from the factory due to other reasons (e.g. antibiotic residues); from this point forward this yield will be referred to as *Herd_Yield*.

Pedigree information

Ancestry information for each cow was obtained from the DairyMIS database and verified using records from the Irish Dairy Recording Co-operative. Holstein UK provided the proportion of NAHF for known sires in the data set. The proportion of NAHF ancestry for foundation cows present on the database in 1990 was calculated as:

$$\text{NAHF}(\text{cow}) = 0.5 \times \text{NAHF}(\text{sire}) + 0.25 \times \text{NAHF}(\text{maternal grandsire}).$$

The youngest maternal grand dams of these cows would have been born at the very least 4 years previously (spring 1986) hence it was assumed that they had no NAHF genes (personal communication, M. Winters, Holstein UK). Also there was no evidence of importation of foreign cows in these herds in this time period. Cows with missing sire or maternal grandsire NAHF information were deemed to have unknown NAHF. Proportion of NAHF for descendants of these cows in the herds in 1990 and in subsequent years was calculated as:

$$\text{NAHF}(\text{cow}) = 0.5 \times \text{NAHF}(\text{sire}) + 0.5 \times \text{NAHF}(\text{dam}).$$

A coefficient of heterosis for each cow was subsequently calculated as:

$$\text{heterosis}(\text{cow}) = [1 - \text{NAHF}(\text{sire})] \times [\text{NAHF}(\text{dam})] + [\text{NAHF}(\text{sire})] \times [1 - \text{NAHF}(\text{dam})].$$

The sire and maternal grandsire predicted difference for milk yield (PD_{MILK}) survival (PD_{SURV}) and calving interval (PD_{CI}) were obtained from the Irish Cattle Breeding Federation in February 2003. Base values on which the sire proofs for the three traits were estimated were 5227 kg for milk yield (first lactation equivalent), 79.9% for survival (average across the first three lactations) and 376.5 days for calving interval (average across the first three lactations). The pedigree index (PI_{MILK}) for each cow was calculated as:

$$\text{PI}_{\text{MILK}}(\text{cow}) = 0.5 \times \text{sire PD}_{\text{MILK}} + 0.25 \times \text{maternal grandsire PD}_{\text{MILK}}.$$

The resulting PEDIGREE data set contained 4362 individual cows with NAHF proportion of which 2781 had individual PI_{MILK} . In total, 3950 cows had predicted difference information on their sires. Unavailability of records for predicted difference proofs for the older maternal grandsires or less

prevalent sires reduced the number of records of cows with actual PI_{MILK} .

Statistical analyses

Two different approaches to statistical analysis were carried out: mixed model analysis and survival analysis.

Mixed model analysis. This analysis was used to determine the association between calving period, parity, CSI, PI_{MILK} , NAHF, MILK_{YLD} , coefficient of heterosis and the dependent binary calving outcome variables (CALV1 and CALV12). The merging of the pedigree, calving and milk production files resulted in Data set_1 containing 7524 records on 2525 individual cows with complete information on CALV1, NAHF, PI_{MILK} and MILK_{YLD} (7273 records on 2497 cows with CALV12 information).

Instead of discarding the remaining 3261 records on 1670 cows with information on CALV1 (3,015 with CALV12), NAHF and sire predicted difference for milk yield but missing information on individual cow PI_{MILK} and MILK_{YLD} , another data set was constructed (Data set_2). The available information was used to simulate PI_{MILK} for the cows with missing information for this trait. Predicted index for milk yield for these animals was estimated as follows:

$$\text{PI}_{\text{MILK}}(\text{cow}) = 0.5 \times \text{PD}_{\text{MILK}} + 0.5 \times \overline{\text{PI}_{\text{MILK}}}$$

where $\overline{\text{PI}_{\text{MILK}}}$ is the average PI_{MILK} of dams of contemporary cows in the herd born in the same year as the cow with missing PI_{MILK} .

It was decided that the availability of overall herd production data in each year of the study coupled with the available individual milk yields on a sizeable proportion of cows presented an opportunity to examine the merits of the data augmentation technique in order to predict missing individual milk yields of their herd contemporaries in Data set_2. Data augmentation refers to methods of constructing iterative algorithms via the introduction of unobserved data or latent variables. For stochastic algorithms, the method was popularized in the statistical literature by Tanner and Wong (1987). This process is described in more detail below using the current data set. While it is acknowledged that iterative data augmentation cannot replace real data the method has been used with confidence in other research disciplines, consumer finance and behaviour (Kennickell, 1991; Chen and Yang, 2003) and in gene discovery (Shane *et al.*, 2004). However, no previous use of this technique in relation to dairy cattle studies was found in the literature.

Using the existing milk yields in Data set_1, a single iteration of PROC MIXED (Statistical Analysis Systems Institute (SAS), 2004) was used to determine the effects of herd, year, calving month, parity, NAHF and PI_{MILK} on MILK_{YLD} . A forward-backward stepwise procedure was used to create a model that explained the greatest variation in MILK_{YLD} . The entry and exit significance level was set at $P < 0.05$ based on the *F* test. Biologically plausible interactions were also tested as were the significance of higher

order covariates. The final model included the fixed effects of herd, year, month of calving, parity, a herd by year interaction, PI_{MILK} as a linear effect and a quadratic regression on NAHF. Cow was included as a random effect. A permanent environmental effect was sampled for each cow using the permanent environmental variance estimated by PROC MIXED. Temporary environmental effects were sampled for each lactation using the residual variance estimated by PROC MIXED. The solutions estimated for the above effects were then used to separately predict individual cow $MILK_{YLD}$ in Data set_2 for cows with no recorded $MILK_{YLD}$ but with all other fixed effects. Data set_1 and Data set_2 were then combined (Data set_12) (see Table 1 for cow numbers and records available in each data set created).

Iterative data augmentation. As mentioned previously annual milk yield at a herd level was also available for all herds in all years (Herd_Yield). Predicted $MILK_{YLD}$ per cow were then additively scaled up within herd-year until their sum plus the constant sum of their contemporary cows within herd-year with true $MILK_{YLD}$ equalled the recorded Herd_Yield (i.e. the true $MILK_{YLD}$ originally from Data set_1 were not scaled and remained the same throughout). The PROC MIXED model was then subsequently refitted using all cows in Data set_12, with actual records for animals that had such and predicted records for animals that originally had no actual observations, producing a new set of solutions for the effects of herd, year, calving month, parity, NAHF and PI_{MILK} on $MILK_{YLD}$. These new solutions were then used to repeat the whole process of predicting and scaling $MILK_{YLD}$ for the cows that originally had no $MILK_{YLD}$ records.

A SAS macro was invoked to generate 15 000 iterations of the above process. As well as including PROC MIXED to predict $MILK_{YLD}$ for cows that had no actual observation, a GLIMMIX macro, with a logit link function and accounting for a binomial error distribution, was included within the main macro. The GLIMMIX macro uses iteratively reweighted likelihood to fit the generalized linear mixed model (Wolfinger and O'Connell, 1993; Little *et al.*, 1996). It allows, among others, fitting of a logit link function and binomial error term to account for the binary nature of the dependent variable. By default, GLIMMIX uses restricted

maximum likelihood when random components are involved. The macro calls PROC MIXED iteratively until convergence, which is decided using the relative deviation of the variance/covariance parameter estimates. An extra-dispersion scale parameter is estimated by default.

Subsequent to completion of the first 15 000 iterations (burn-in), and at every subsequent 100th iteration, the GLIMMIX macro was called to estimate the effects of calving month, CSI, parity, NAHF, PI_{MILK} , $MILK_{YLD}$ and coefficient of heterosis, on both CALV1 and CALV12. Milk yield included in this analysis was the true $MILK_{YLD}$ of cows with such and the most recently predicted $MILK_{YLD}$ (from the PROC MIXED analysis) of cows that originally had no observed $MILK_{YLD}$. Every 100th iteration was extracted to minimize the potential bias arising from the co-variation between adjacent iterative solutions from PROC MIXED.

Similar to the estimation of $MILK_{YLD}$, preliminary analysis was performed to determine the most suitable model to investigate CALV1 and CALV12. Following the sequential inclusion of each term into the prediction model, a multicollinearity test was undertaken in PROC REG (SAS, 2004) to determine the collinearity or lack thereof, between explanatory variables. This test was necessary as moderate to strong relationships was expected among some explanatory variables; a correlation of 0.76 and 0.79 was estimated between NAHF and PI_{MILK} in Data set_1 and Data set_12, respectively. The correlation between both NAHF and PI_{MILK} and $MILK_{YLD}$ was positive but < 0.20 in either data set. The existence of collinearity was deduced from the variance inflation factor and the condition index. The resulting condition indexes found with NAHF, PI_{MILK} and $MILK_{YLD}$ included in the model were all less than 13 indicating collinearity was not a problem between any of the independent variables. Hence, the variation in PI_{MILK} for a given level of NAHF and *vice versa* was deemed sufficient to allow inclusion of both variables in the model; the correlation between PI_{MILK} and NAHF would suggest that NAHF explained 62% of the variation in PI_{MILK} . Additionally, the change in solutions of explanatory variables was monitored with the sequential inclusion of additional variables into the prediction model.

The significance of each explanatory variable (or biologically plausible interactions) on CALV1 or CALV12 was determined from the 95% confidence interval of the solutions derived from the iterative procedure previously described. The applicability of higher order covariates was also established from both the 95% confidence interval of the solutions and also from a graphical comparison of each order. The final model included the fixed effects of herd, year, month of calving, parity, a herd by year interaction, a quadratic regression on CSI, and linear effect of $MILK_{YLD}$, PI_{MILK} , NAHF and coefficient of heterosis. Table 2 shows the results of the model building steps with sequential inclusion of variables and their effect on CALV1.

Survival analysis

Survival analysis was carried out on all cows with at least one calving record across the 14 herds over the 12 years.

Table 1 Data sets created and number of cows and records in each data set

	Data set	
	No. of cows	No. of records
Total	5580	
FERTILITY	4434	14 019
PEDIGREE	4362	
-with NAHF	4362	
-with PI_{MILK}	2781	
-with sire PD_{MILK}^{\dagger}	3950	
MILK	3179	9383
Data set_1	2525	7524
Data set_2	1670	3261
Data set_12	4195	10 785
SURVIVAL	5580	5580

[†] Sire PD_{MILK} = sire predicted difference for milk yield.

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Table 2 Sequential testing of the effect of independent variables on calving rate to first service using Data set_12 after 15 000 iterations

Model [†]	Variable [‡]		
	MILK _{YLD}	PI _{MILK}	NAHF
MILK _{YLD}	– 0.00 009		
MILK _{YLD} , PI _{MILK}	– 0.00 009	– 0.00 026	
MILK _{YLD} , NAHF	– 0.00 009		– 0.00 118
PI _{MILK} , NAHF		– 0.00 036	– 0.00 059
MILK _{YLD} , PI _{MILK} , NAHF	– 0.00 009	– 0.00 020	– 0.00 070

[†] MILK_{YLD} = phenotypic milk yield; PI_{MILK} = pedigree index for milk yield; NAHF = Proportion of North American Holstein Friesian genes.

[‡] All models also included effects of herd, year, herd × year interaction, calving month, CSI, CSI × CSI and parity.

Information was available on a total of 5580 animals of which 4362 had NAHF information. Animals with unknown NAHF ($n = 1218$) were also included in the analysis but were coded as unknown percentage NAHF. Survival parameters were estimated by maximum likelihood using 'The Survival Kit' software (Ducrocq and Solkner, 1998a and b). The dependent variable was the survival time in days from first calving to end of productive life. The end of productive life was defined as the actual date of sale or death. If the actual date of sale or death was not indicated in the data set (4% of records), the date of removal was assumed to be 31 December in the year of her last recorded calving. Animals sold as surplus, for reasons unknown, or those alive on 31 December 2001 were treated as censored (37%).

Preliminary analysis was carried out on the shape of the baseline hazard function. The Kaplan-Meier estimator of the survival function and the Nelson-Aalen estimator of the cumulative hazard function revealed that the underlying survival distribution was non-parametric; no effects were included in the model of analysis. Therefore, survival analysis was undertaken using a proportional hazards Cox model (Cox, 1972).

The proportionality of hazards across both breeds and herds was also determined by estimating the hazard function of each breed and herd separately. Relative hazard functions were close to parallel suggesting no need for stratification. The proportional hazards model used describes the hazard of culling at any time:

$$t : h[t; \mathbf{x}, \mathbf{z}(t)] = h_0(t) \exp[\mathbf{x}'\beta + \mathbf{z}'(t)\gamma]$$

where $h_0(t)$ = baseline hazard function, \mathbf{x} = vector of time-independent covariates, \mathbf{z} = vector of time-dependent covariates, and β and γ = vectors of corresponding regression coefficients.

The significance of effects in the model was tested by minimizing the Akaike's information criterion (AIC) which was defined as:

$$\text{AIC} = -2\text{Log}L + 2p$$

where $\text{Log}L$ is the log-likelihood and p is the number of parameters in the model.

Using the above criteria, a forward selection procedure was performed to identify the extra information attributable to each trait over and above that already explained in the model. Effects demonstrating the largest effect on the AIC were sequentially added to the model. Time independent covariates investigated in the models included NAHF, PI_{MILK} and coefficient of heterosis as continuous variables. Higher order regressions were also tested for significance in the model. A herd × year interaction was included as a time-dependent covariate. The final model consisted of a herd × year time-dependent covariate with a quadratic regression on NAHF and both PI_{MILK} and heterosis included as continuous variables.

Additionally, to facilitate the construction of survival curves animals with known NAHF were categorized into one of three breed groups: 0 to 25% NAHF ($n = 1236$), 26 to 50% NAHF ($n = 1399$), greater than 50% NAHF ($n = 1727$).

Results

Herds

The average stocking rate (range) and nitrogen (N) used (range) on the farms over the 12 years was 2.90 livestock units (LU) per ha (2.00 to 3.85) and 324 kg N per ha (155 to 464), respectively. There was a tendency toward a reduction in stocking rate over time while N usage remained unchanged over the period. There was no trend in the level of concentrate feeding level (measured on a herd basis each year) over the period 1990 to 2001. The level of concentrate supplementation over the period averaged over all herds was 613 kg per cow (ranging from 407 kg in 1997 to 712 kg in 1995).

Phenotypic and genetic trends in milk production, calving rate and fertility performance

Table 3 shows the phenotypic trends in herd milk production and lactation length from DairyMIS. Performing a simple linear regression through the yearly estimates indicated that phenotypic milk production per cow increased on average

Table 3 Phenotypic herd average milk production (kg per cow), fat concentration (g/kg), protein concentration (g/kg) and lactation length (days), in herds recorded on the Dairy Management Information System (DairyMIS) for years 1990 to 2001

Year	Milk yield (kg)	Fat (g/kg)	Protein (g/kg)	Lactation length (days)
1990	5033	36.3	32.1	274
1991	5011	36.7	32.0	271
1992	4992	37.4	32.4	273
1993	5307	37.3	32.6	273
1994	5383	37.7	32.7	280
1995	5490	37.6	32.2	269
1996	5594	37.7	32.7	255
1997	5629	37.8	32.8	262
1998	5504	38.4	33.2	257
1999	5605	38.4	33.5	257
2000	5609	38.3	33.7	257
2001	5775	38.4	33.9	261

by 69 (s.e. 7.8) kg/year, increasing from 5033 kg per cow in 1990 to 5775 kg per cow in 2001. Over the 12 years milk fat and protein concentration increased by 0.02 (s.e. 0.002) g/kg per year, while average lactation length decreased by 1.9 (s.e. 0.49) days/year. The trend toward shorter lactation length may have one of two causes. Firstly due the seasonal nature of production. It is common practice for these farmers to dry off the entire herd over a 2- to 3-week period in November/December. Cows calving late in any particular year due to poor reproductive performance the previous year will therefore have reduced lactation lengths. Secondly the study period occurred in a time of milk quota restriction at farm level. The quota year commences on 1 April each year, which is out of synchrony with the calving season in Ireland. Certain farmers may have anticipated quota availability problems and hence may have opted to dry-off earlier in the year as opposed to reducing cow numbers.

Table 4 shows the trends in fertility performance for the cows in the DairyMIS herds from 1990 to 2001, calculated using the CALVING data set. When a linear regression was fitted through the mean annual performances between 1990 and 2001 there was a significant decline in CALV1 (−0.96 (s.e. 0.165) percentage units per year), CALV12 (−0.84 (s.e. 0.134) percentage units per year) and average parity (−0.10 (s.e. 0.013) lifetime lactations per year). There was no consistent trend in ICI, however there was a significant increase in NS (+0.022 (s.e. 0.0053) services per year), replacement rate (+0.84 (s.e. 0.0001) % per year) (expressed as a percentage of all cows calved and inseminated in a particular year) and percentage of cows culled due to infertility (+2.7 (s.e. 0.004) % per year) (expressed as a percentage of cows culled).

Between the years 1990 and 2001 the proportion of NAHF genes increased annually by 5.5 (s.e. 0.179) percentage units from 8% in 1990 to 63% in 2001. Over the 12 years PI_{MILK} of the cows increased by 25 (s.e. 0.99) kg/year.

Table 4 Phenotypic herd averages of calving rates to first service, calving rate to first and second service, number of services per cow, intercalving interval, average parity, replacement rate and percentage of cows culled due to infertility in herds recorded on the Dairy Management Information System (DairyMIS) for years 1990 to 2001[†]

Year	CALV1 (%)	CALV12 (%)	NS (no.)	ICI (days)	PAR (no.)	REP (%)	CIF (%)
1990	55.2	76.8	1.54	370	4.3	16	27
1991	53.0	74.3	1.65	374	4.6	18	17
1992	52.5	76.2	1.63	368	4.3	19	47
1993	52.1	77.0	1.67	372	4.0	21	28
1994	48.3	73.5	1.77	377	4.0	18	23
1995	49.4	74.3	1.66	370	3.9	24	31
1996	44.4	69.9	1.70	375	3.7	22	29
1997	48.7	71.3	1.70	377	3.5	25	35
1998	49.9	70.1	1.71	371	3.4	25	45
1999	46.2	68.1	1.87	371	3.5	25	52
2000	42.8	67.3	1.89	375	3.5	26	54
2001	44.0	70.0	1.75	372	3.5	24	53

[†] CALV1 = calving rate to first-service; CALV12 = calving rate to first and second-service; NS = number of services per cow; ICI = intercalving interval; PAR = average parity; REP = replacement rate; CIF = percentage of cows culled due to infertility out of all cows culled.

Figure 1 shows the trend in PD_{SURV} and PD_{CI} of the sires of the cows in the herds over the 12-year period. The PD_{SURV} of sires declined by 0.12 (s.e. 0.009) % per year, while PD_{CI} increased by 0.46 days/year.

Relationship between PI_{MILK} and NAHF variables and $MILK_{YLD}$

Table 5 summarizes the associations between the independent variables and $MILK_{YLD}$, from the analysis of Data set_1 and the mean of 100 estimates from the 10 000 iterations of Data set_12 after the initial 15 000 iteration burn-in. As expected calving period had a large effect on overall level of $MILK_{YLD}$ due to differential lactation lengths. Parity also had a large effect on $MILK_{YLD}$ with first and second parity cows respectively producing 1378 and 483 kg less $MILK_{YLD}$ than cows in three or more lactations. The results suggest that for an increase in PI_{MILK} (i.e. half the breeding value) of 1 kg there was an increase in $MILK_{YLD}$ of 1.88 kg or the increase in PI_{MILK} explained all the increase in phenotypic milk yield over the period of the study.

Relationship between $MILK_{YLD}$, PI_{MILK} and NAHF variables and CALV1 and CALV12

Preliminary analysis indicated that the relationships obtained between independent variables $MILK_{YLD}$, PI_{MILK} and NAHF and dependent variables, CALV1, and CALV12 were similar for both Data set_1 and Data set_12. Furthermore there was a reduction in the standard errors of the estimates derived using Data set_12 as opposed to Data set_1. Therefore only results for Data set_12 are presented in Table 6, which summarizes the associations between the independent variables and dependent variables, CALV1, and CALV12, plus the 95% confidence interval for the estimates. The confidence intervals are based on the results of 100 outputs (1 in every 100th iteration outputted from 10 000 iterations after the initial 15 000 burn-in iterations). Cows calving in January and February had a greater likelihood of a successful CALV1 and CALV12 than cows calving in March or in April-May. Longer calving to service intervals of 10 days increased the likelihood of success to CALV1 and CALV12 by 1.6 and 1.8 percentage units respectively. Second parity cows had a lower likelihood of a successful CALV1 compared with cows in third or higher parity. First and second parity cows had reduced likelihood

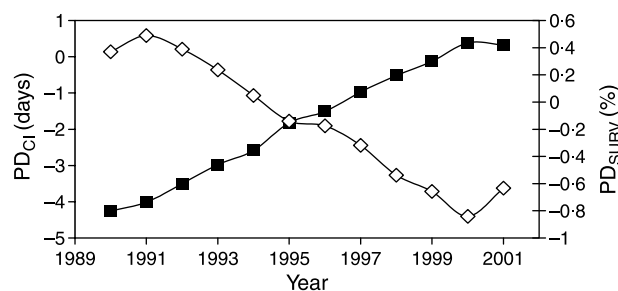


Figure 1 Genetic trends in predicted difference for calving interval (PD_{CI} (days) = ■) and survival rate (PD_{SURV} (%) = ◇) based on sires of cows in herds recorded on the Dairy Management Information System for years 1990 to 2001.

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Table 5 Model estimates from PROC MIXED analysis, showing associations between model parameters and dependent variable milk yield from Data set_1 and the mean of 10 000 runs of Data set_12

	Level [†]	Data set_1		Data set_12	
		Estimate	95% CI [‡]	Mean of estimates	95% CI [‡]
Intercept		5051.8	4918.6, 5185.0	5069.5	5019.1, 5114.9
Calving period	Jan-Feb	1041.5	991.6, 1091.4	1017.7	985.0, 1043.2
	Mar	613.0	560.8, 665.2	603.9	565.7, 640.7
Parity	1	-1378.1	-1422.7, -1333.5	-1377.0	-1385.2, -1330.1
	2	-483.3	-523.7, -442.9	-479.4	-501.1, -454.8
PI _{MILK} [§]	(per 1 kg inc.)	1.882	1.566, 2.198	1.804	1.676, 1.925
NAHF [§]	(per 1% inc.)	7.025	3.296, 10.754	7.536	5.710, 9.258
NAHF × NAFH [§]	(per 1% inc.)	-0.111	-0.152, -0.070	-0.110	-0.132, -0.088

[†] Reference category: calving period = April-May; parity = 3 + ; inc. = increase.

[‡] For Data set_1, 95% CI: calculated using the formula (estimate $\pm 1.96 \times \text{s.e.}$); for Data set_12, 95% CI: calculated from 100 estimates of Data set_12 (1 in every 100 from 10 000 iterations of Data set_12).

[§] PI_{MILK}=pedigree index for milk yield; NAFH = proportion of North American Holstein-Friesian genes.

of success to CALV12 compared with third and greater parity cows. Increased levels of PI_{MILK}, MILK_{YLD} and NAFH were all found to have a negative association with both CALV1 and CALV12. As mentioned previously the estimates reported in Table 6 were similar to those achieved using Data set_1, i.e. the effects of PI_{MILK}, MILK_{YLD} and NAFH on CALV1 using Data set_1 were -0.00035, -0.00008, and -0.00052, respectively. The two calving traits were positively associated with increasing coefficient of heterosis.

Survival analysis

In the data set analysed 1248 records (22%) were left truncated (first calving date occurred prior to 1 January 1990) and 2054 (37%) were right censored (still alive at the end of the study period, or sold as surplus or reasons unknown). Table 7 shows the hazard estimates and level of significance for the independent variables NAFH, PI_{MILK} and coefficient of heterosis. Figure 2 illustrates the change in risk of culling with increasing NAFH genes and with increasing coefficient of heterosis. Increasing levels of NAFH were associated with increased risk of culling up to 87.5% NAFH after which the risk started to plateau. Figure 3 shows the effect of proportion of NAFH genes on the predicted survival

curves for 3 categories of percentage NAFH. The curves show a large differential in survival as influenced by percentage NAFH.

Discussion

Trends in milk production

The analysis of this data set has shown that the more recent North American-derived Holstein cows had increased milk yield in comparison to their British Friesian predecessors. The breeding objective used in Ireland from 1990 to 2001 was the relative breeding index (RBI); this included genetic merit for milk, fat, and protein yield as well as protein content (Irish Cattle Breeding Federation, 1999). The increase in milk production per cow over the 12 years (69 kg per cow per year) in the present study is higher than the increase reported in Irish milk recorded herds for the same period (5400 to 5954 kg or 36-kg increase per year) (V. Olori, personal communication), however, the latter yields are 305-day yields whereas the yields in this study are based on actual lactation yields (an average lactation length of 265 days). The results in Table 5 indicate that the increase in genetic merit for milk yield explains all of the increase in phenotypic milk yield over the period of the

Table 6 Model estimates from GLIMMIX macro analysis of data set_12, showing associations between model parameters and dependent variables calving rate to first service and calving rate to first and second service[†]

	Level [‡]	CALV1		CALV12	
		Mean of estimates	95% CI	Mean of estimates	95% CI
Intercept		-2.0926	-2.2350, -1.9438	-0.7010	-0.8630, 0.5124
Calving period	Jan-Feb	0.4633	0.4407, 0.4872	0.4902	0.4629, 0.5206
	Mar	0.3114	0.2966, 0.3283	0.2985	0.2803, 0.3190
CSI	(per 1 day inc.)	0.0390	0.0387, 0.0394	0.0336	0.0332, 0.0340
CSI × CSI	(per 1 day inc.)	-1.8×10^{-4}	-1.8×10^{-4} , -1.7×10^{-4}	-1.6×10^{-4}	-1.6×10^{-4} , -1.6×10^{-4}
Parity	1	-0.0027	-0.0463, 0.0369	-0.085	-0.1408, -0.0389
	2	-0.1340	-0.1496, -0.1195	-0.0494	-0.0686, -0.0333
MILK _{YLD}	(per 1 kg inc.)	-7.0×10^{-5}	-1.0×10^{-4} , -4.1×10^{-5}	-9.1×10^{-5}	-1.3×10^{-4} , -5.7×10^{-5}
PI _{MILK}	(per 1 kg inc.)	-3.2×10^{-4}	-3.7×10^{-4} , -2.5×10^{-4}	-2.3×10^{-4}	-2.9×10^{-4} , -1.6×10^{-4}
NAHF	(per 1% inc.)	-0.0018	-0.0019, -0.0017	-0.0005	-0.0007, -0.0004
Heterosis	0 to 100%	0.0019	0.0019, 0.0020	0.0020	0.0019, 0.0021

[†] CALV1 = calving rate to first-service; CALV12 = calving rate to first and second-service; CSI = calving to service interval; MILK_{YLD}=phenotypic milk yield; PI_{MILK}=pedigree index for milk yield; NAFH = proportion of North American Holstein-Friesian genes; heterosis = coefficient of heterosis.

[‡] Reference category: calving period = April-May; parity = 3 + ; inc. = increase.

Table 7 Estimates, standard errors and significance levels for independent variables from survival analysis showing the effect of the variables on the risk of culling

Variable [†]	Estimate	s.e.	Significance
NAHF (per 1% inc.)	0.0176	0.00414	***
NAHF × NAFH (per 1% inc.)	-9.9×10^{-5}	-4.8×10^{-5}	*
PI _{MILK} (per 1 kg inc.)	-0.0004	0.00024	
Heterosis (per 1% inc.)	-0.0043	0.00122	***

[†] Inc. = increase.

study. A similar conclusion is evident when comparing the change in genetic merit for milk yield in the Irish national cow population relative to the changes in national phenotypic milk yield over the years in the present study. This suggests that intake capacity and/or the energy content of grazed grass is a limitation to the amount of milk produced. In support of this, Kennedy *et al.* (2002) reported a higher response to concentrate input in cows of higher genetic merit for milk production thereby suggesting the necessity for a refinement of nutritional feeding if the objective is to maximize milk yield from cows of high genetic merit for milk yield.

Trends in calving rate

The calving rate to first service observed for 1990 was similar to that obtained in a number of previous surveys (Crowley *et al.*, 1967; Cunningham *et al.*, 1978; Roche *et al.*, 1978), all of which indicated calving rates to first service of 60% or greater. The decline in fertility performance observed in this study from 1990 to 2001 as assessed using calving rates is similar to that observed in other countries. In the United Kingdom, Royal *et al.* (2000) reported that between 1975–1982 and 1995–1998, pregnancy rate to first service declined from 55.6% to 39.7%, or a decline of almost 1% per year. In the USA, Butler (1998) showed a decline in first service conception rate from approximately 65% in 1951 to 40% in 1996. Today inter calving intervals in the United States average 435 days (Lucy, 2001), in Canada they average 411 days (Fatehi and Schaeffer, 2003), while in The Netherlands they average 405 days (Royal Dutch Cattle Syndicate, 2000).

In the present study the average inter calving intervals did not show any recognizable trend from 1990 to 2001. However there was an increase of 0.46 days in the genetic merit for calving interval PD_{CI} of the sires of cows in the herds which should have indicated toward longer calving intervals. The discrepancy may be explained by increases in replacement rate and culling for infertility in these herds. Animals do not get a chance to calve at long intervals in seasonal calving herds because if they are not pregnant by the end of the breeding season then they are culled from the herd at the end of the year, hence the more animals not in calf then the higher the replacement rate required to maintain cow numbers the following season. This is also reflected in the percentage of cows culled due to infertility reasons. The increase of 0.46 days in PD_{CI} of the sires of cows in the herds is similar to that reported previously by Olori *et al.* (2002) for Holstein-Friesian sires in Ireland. Olori *et al.*

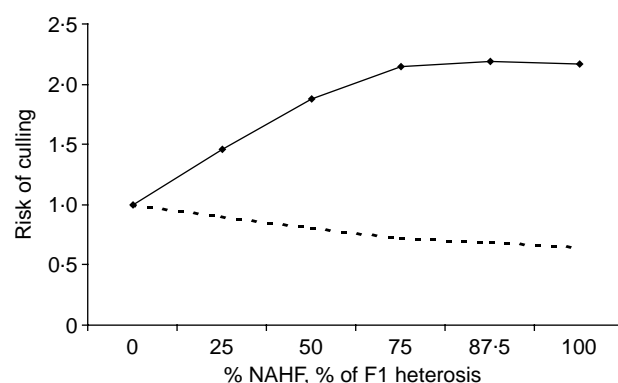


Figure 2 Relative risk of culling with increasing level of NAFH — (corrected for heterosis and PI_{MILK}) and increasing coefficient of heterosis --- (corrected for level of NAFH and PI_{MILK}).

(2002) showed that for sires by birth years 1984 to 1995 PD_{CI} increased by 0.14 days per year.

The USA and Dutch dairy industries primarily consist of continuously calving herds; thus reproductive efficiency can be sacrificed for gains in milk production productivity. However, in countries that depend on seasonal calving, this reduced reproductive efficiency imposes a tremendous challenge to the sustainability of the system. Late calving cows caused by failure to conceive to first or second service the previous year impose management difficulties for farmers as these cows will be out of synchrony with the rest of the herd with regard to feeding management and breeding practices throughout the duration of the year. Hence more intensive culling rather than extending the breeding season is often the more likely practice in order to maintain compact calving of the herd.

Genetic and phenotypic relationships between genotype, milk production and calving rate

Results suggest that the North American-derived Holstein cows had poorer fertility and lower survival in comparison to their British Friesian predecessors. The authors have attempted to decipher the relationship of three interlinked variables (PI_{MILK} , $MILK_{YLD}$, NAFH) both with each other and with subsequent herd calving performance. The increases in milk yield that occurred on these farms would most likely

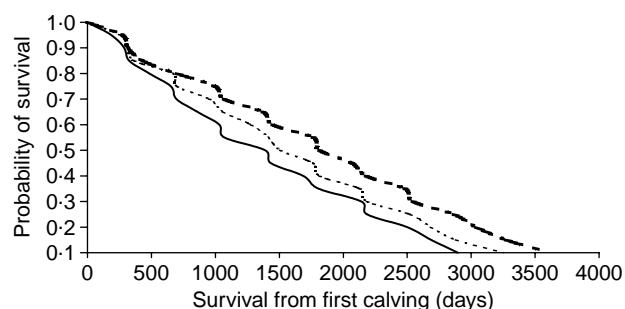


Figure 3 Effect of proportion of North American genes — = less than 26% NAFH; --- = 26 to 50% NAFH; . . . = greater than 50% NAFH; on the predicted survival curves of cows in 14 DairyMIS herds from 1990 to 2001.

not have occurred at the same rate without the increase in NAHF genes brought about through selection of animals for superior PI_{MILK} . Hence farmers increased the NAHF genes in their cows indirectly by selecting for increased PI_{MILK} with the goal of increasing phenotypic milk yield per cow. The effects of these variables become even more difficult to ascertain when non-additive effects of heterosis are affecting both $MILK_{YLD}$ and likelihood of conception in different crosses of the British Friesian and NAHF. However, the partitioning out of the effects of these variables on calving rates may provide valuable insight into how to proceed with future breeding policies and selection of dairy cattle so that increases in phenotypic milk yield can be achieved without the indirect consequences of further reduced fertility performance.

In more recent times evidence has arose implicating genetic selection in dairy cattle primarily for higher milk production as a causal factor of reduced fertility (Hoekstra *et al.*, 1994; Evans *et al.*, 2002; Royal *et al.*, 2002) and reduced health (Emanuelson *et al.*, 1988; Pryce *et al.*, 1998). There is evidence that cows of high genetic merit mobilize more body tissue in early lactation than cows of average genetic merit (e.g. Pryce *et al.*, 2001). Thus, even though all cows mobilize body tissue in early lactation, there is a greater predisposition for cows of high genetic merit to do so (Pryce *et al.*, 2004). Pryce *et al.* (2004) suggested that breeds selected for high production are more likely to be in extreme negative energy balance in early lactation and thus genetic correlations between production and fertility will be more unfavourable in these breeds. Gutierrez *et al.* (2006) in trials involving spring-calving cows found that selection on predicted breeding values for milk production was associated with a longer interval from parturition to first ovulation. Similar to the present study this effect of breeding value for milk production was found to be independent of phenotypic milk production. There is evidence of negative genetic and phenotypic correlations between milk production and fertility in other breeds also. Grosshans *et al.* (1997) found antagonistic genetic correlations between production and fertility in both Jersey and Holstein-Friesian cows in seasonal calving New Zealand dairy herds. However, there was also a breed effect reported with Jersey cows displaying superior fertility.

Simultaneous adjustment for phenotypic milk yield, genetic merit and heterosis in the current study did not fully account for the negative impact of increasing NAHF on calving rates. Hoekstra *et al.* (1994) and Harris and Kolver (2001) both reported declining fertility performance with introgression of NAHF genes but it was not differentiated whether it was increased genetic merit for milk yield or NAHF *per se* which was the primary cause. Lindhe and Philipsson (1998) also reported that the genetic correlation between fertility and protein yield was more highly negative for Swedish Black and Whites with sires that were Holstein than for those with Swedish sires, indicating a 'Holsteinization' effect on female fertility. However, Pryce *et al.* (2004) interpreted the cause of the above results of Lindhe and Philipsson (1998) as possibly due to more intense selection for milk production in the Holstein breed. More recently, Horan *et al.* (2004) reported large differences in reproductive performance between three strains of Holstein-Friesian involved in

a spring calving grass-based system of milk production. The strain with poorest reproductive performance were those with the poorest genetic merit for fertility traits, highest proportion of NAHF and highest genetic merit for milk production while those with the best reproductive performance were those with the highest genetic merit for fertility, lowest proportion of NAHF genes and genetic merit for milk production. In contrast to the above, a study by Royal *et al.* (2002) comparing Holstein and British Friesian cows found no significant effect of NAHF on commencement to luteal activity which has been linked to traditional measures of fertility (Darwash *et al.*, 1997).

Another possible theory often hypothesized to explain declines in fertility is inbreeding depression. Inbreeding can lead to a decline in performance in traits associated with fitness, such as reproductive rate and disease resistance (Simm, 1998). Mark *et al.* (2002) in an analysis of Holstein pedigrees from 24 countries reported the effective population size of the breed reached its lowest level in 1994 when it was 55, which was below the optimum effective population size of 80 recommended by Goddard (1992). The effective population size subsequently increased to 449 for bulls born in 1999. Current rates of inbreeding in the active bull population influences the rate of inbreeding in the commercial population in subsequent generations.

The positive effect of heterosis in crossbred cows on CALV1 and CALV12 found in this study has also been reported in other dairy populations. Harris *et al.* (2000) found substantial positive heterosis estimates on pregnancy rate to first service and survival in North American Holstein Friesian-Jersey crossbreds and to a lesser extent in New Zealand Friesian-North American Holstein Friesian crossbreds. Wall *et al.* (2005) found that heterosis had a favourable effect on days to first service and calving interval in F1 crosses of Holstein-Friesian \times British Friesian cows compared with the average of pure Holstein and British Friesians. In the present study the average level of NAHF genes for all cows in the herds in 2001 was 63% whereas for first parity animals it was 70%. Hence, heterosis could still be having a positive impact on calving rates. Continued use of Holstein Friesian sires of high genetic merit for milk yield without simultaneous selection for fertility traits in the present study may result in further reductions in CALV1 and CALV12 as NAHF proportion increases closer to 100%, and as the positive effects of heterosis disappear.

The decline of 0.12% per year in PD_{SURV} of the sires of cows in the herds is similar to that reported previously by Olori *et al.* (2002) for Holstein-Friesian sires in Ireland. Olori *et al.* (2002) showed that for sires by birth years 1984 to 1995, survival rate declined by 0.05% per year. In the present study increased proportion of Holstein-Friesian genes resulted in lower survival as indicated by the higher hazard ratio. Harris *et al.* (2000) using a Weibull parametric proportional hazards regression model showed similar results in the New Zealand cow population. Using records from the New Zealand national database Harris and Kolver (2001) showed that North American-derived Holstein Friesian cows were heavier, produced more milk volume and protein yield,

had lower concentration of fat and protein, had poorer fertility and survival than New Zealand Holstein Friesian cows. Corroborating results from the present study, Berry *et al.* (2005a) also reported an increased risk of culling in New Zealand as the proportion of overseas Holstein-Friesian genes increased up to a level of 80% Holstein-Friesian after which the risk of culling declined. It was suggested that cows with a high proportion of overseas Holstein-Friesian genes may have been retained for reasons other than their innate ability to survive.

Future direction

Consistent features of the farms in this study over the 12 years investigated included spring calving, primarily grass based diets, low to medium levels of concentrate supplementation and herd average lactation lengths between 260 and 280 days. However, the cows in these herds evolved from primarily British Friesian to primarily Holstein-Friesian in genetic makeup, which contributed to higher yields of milk, fat and protein but with a reduction in calving rates. Further reproductive loss may become unsustainable and force these farmers into an undesirable situation of having to source replacements from elsewhere to maintain calving patterns or else extend the length of breeding season and cope with more extended calving patterns.

Sire selection based on simultaneous improvement of milk production and fertility/survival may allow the sustainability of seasonal calving systems. Good fertility is imperative for all systems of dairy production, irrespective of seasonal or continuous calving. The focus of breeding in countries with large Holstein populations has shifted dramatically in recent years whereby the majority of breeding programs now include functional traits related to health and fertility in addition to selection for milk production (Miglior *et al.*, 2005). Experience in Scandinavian countries has shown inclusion of fertility traits in a selection index have maintained or improved reproductive performance over a similar time period (Philipsson and Lindhe, 2003). Model calculations show that despite the relatively low heritability of most fertility measures, there is sufficient genetic variation to make it worthwhile including in an index of total economic merit (Pryce and Veerkamp, 2001). Given the size of the Holstein Friesian population worldwide and the current endeavour to include traits predicting fertility performance it could be argued that the Holstein-Friesian may address and reverse the trends in fertility performance relatively quickly. In Ireland fertility has a high economic weight relative to milk production traits due Ireland's reliance on seasonal calving systems and recently dairy cattle breeding objectives combining milk production, survival and calving interval for pasture based systems in Ireland have been established (Veerkamp *et al.*, 2002). The relative emphasis placed on milk production and fertility indicator traits (calving interval and survival) in the initial index was 69% and 31% (Veerkamp *et al.*, 2002). Two revisions of this index have taken place since its inception and launch to the Irish dairy industry in 2001 (Berry *et al.*, 2004 and 2005b). The current relative emphasis placed on traits in the index (February 2005; Berry *et al.*, 2005b) is 52% milk production, 35% fertility (calving interval and survival), 8% calving ease and 5% on beef merit.

Conclusions

The present study has indicated that the combined effects of increased genetic merit for milk yield, phenotypic milk yield and NAHF genes has resulted in higher overall herd milk production, lower calving rates and lower survival in 14 seasonal spring calving herds. There was an indication of positive heterosis for both calving rate and survival in British-Friesian × North American Holstein-Friesian crossbred cows. The results indicate a necessity for seasonal calving herds to incorporate fertility and survival traits along with traditional production traits in the selection of sires for future herd replacements.

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